Global Ecology and Conservation 17 (2019) e00523

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Winter insomnia: How weather conditions and supplementary feeding affect the brown bear activity in a long-term study

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ARTICLE INFO

Article history:
Received 27 July 2018
Received in revised form 2 January 2019
Accepted 2 January 2019

Keywords:
Anthropogenic food subsidies
Climate change
Denning ecology
Ursus arctos
Winter activity
Winter severity

ABSTRACT

Climate change and anthropogenic food subsidies affect wildlife everywhere in the world. We used a 30-year set of data on winter observations of brown bear *Ursus arctos* to investigate the effects of weather and supplementary feeding on bear winter activity in the Polish Eastern Carpathians. The probability of observations of bears and their signs was negatively correlated with depth of snow cover and positively related to ambient temperature and the amount of supplementary food. We noted an increase in the frequency of bear winter observations over the study period, which might be additionally related to the increasing bear numbers in the study area. Our results provide new insights into the mechanisms of how climate change and supplementary feeding affect the brown bear, a species considered as threatened by human activity. Supplementary feeding seems to disrupt bears' natural responses to winter weather conditions. Limiting the amount of anthropogenic food subsidies may help to mitigate the effect of climate change on wildlife.

1. Introduction

Climate change and anthropogenic food subsidies are important components of global change. There is ample evidence for substantial effects of changing climate on wildlife, including shifts in species distribution, changes in population size, increased spread of wildlife diseases, loss of habitats, shifts in chronology of life-history events, and changes in seasonal behaviors such as migration and hibernation (McCarty, 2001; Parmesan, 2006; Harvell et al., 2009). Climate change affects organisms worldwide, especially in strongly seasonal habitats where shifts in climatic conditions tend to be more dramatic in winter compared to summer (Campbell et al., 2005; Stocker, 2014; Williams et al., 2015). Winter activity in both hibernating and non-hibernating species is strongly influenced by ambient temperature and snow conditions (Watanuki and Nakayama, 1993; Kowalczyk et al., 2003). Thus, changes in winter weather conditions may adversely affect survival and breeding success of hibernating species, as documented in the little brown bat *Myotis lucifungus* and the Alpine marmot *Marmota marmota* (Humphries et al., 2002; Tafani et al., 2013). In addition to climate change, human-derived food has become increasingly

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https://doi.org/10.1016/j.gecco.2019.e00523

available to wildlife, turning into a progressively important issue in nature conservation (Oro et al., 2013). Supplementary feeding is a widespread way of subsidizing wildlife with anthropogenic food, and it is commonly used as a conservation and management tool (Putman and Staines, 2004; Jones et al., 2014). Supplementary feeding has substantial consequences for wildlife ecology, e.g. it affects activity patterns, movements, social interactions, disease transmission and predation risk (Robb et al., 2008; Jerina, 2012; Corcoran et al., 2013; Selva et al., 2014, 2017; Sorensen et al., 2014; Newsome et al., 2015). However, many of the ecological effects and conservation implications of supplementary feeding remain poorly understood (Robb et al., 2008; Selva et al., 2014).

Bears are the largest species which adapted to adverse winter conditions through hibernation. Several studies revealed that both intrinsic (sex, reproductive status, age, body mass) and external factors (food availability, weather) are important in shaping denning behavior in ursids (Manchi and Swenson, 2005; Evans et al., 2016; Pigeon et al., 2016). While the complex mechanisms that drive hibernation patterns in bears remain only partially understood (Manchi and Swenson, 2005; Krofel et al., 2017), the latitudinal pattern in duration of winter dormancy suggests that climatic factors are important in regulating denning chronology (Linnell et al., 2000; Krofel et al., 2017). Up to date, snow conditions, ambient temperature and day length have been suggested as key external factors controlling the denning chronology in bears (Schooley et al., 1994; Manchi and Swenson, 2005; Tøien et al., 2011; Ware et al., 2012; Evans et al., 2016). Bears typically remain in their dens throughout the winter inactivity period, unless disturbed by humans or flooding (Swenson et al., 1997; Linnell et al., 2000; Manchi and Swenson, 2005). Den abandonment may pose an energetic hazard for bears and adversely affect their fitness (Tietje and Ruff, 1980; Linnell et al., 2000). Some of brown bears *Ursus arctos* on Kodiak Island and in Slovenia and black bears *Ursus americanus* have been reported to repeatedly interrupt their denning, even in the midwinter, albeit the reason for that behavior is not clear (Van Daele et al., 1990; Rayl et al., 2014; Krofel et al., 2017). Moreover, while hibernation is an important energy-saving strategy in winter, some bears may not den at all (Linnell et al., 2000). For instance, some brown bears in southern Europe and North America remain active throughout the winter due to either mild weather conditions or availability of forage (Van Daele et al., 1990; Huber and Roth, 1997; Linnell et al., 2000). A growing evidence suggests that food availability in autumn and winter may be especially important in driving the denning chronology and continuousness (Pigeon et al., 2016), as it is supported by observations of brown bears on Kodiak Island entering dens later in areas where sockeye salmon *Oncorhynchus nerka* were available (Van Daele et al., 1990). Supplementary feeding was a plausible cause for interrupted denning of brown bears in Slovenia (Krofel et al., 2017). Supplementary food may constitute one of the most important food sources for brown bears in some areas, especially during the winter, as illustrated in the Carpathians (Kavčič et al., 2015; Štofík et al., 2016).

In this paper, we investigate the frequency of winter observations of brown bears and signs of their activity in the Polish part of the Carpathians in the period from 1987 to 2016. Here, brown bears during winter are subject to moderate weather conditions and supplementary feeding (Selva et al., 2017). We hypothesize that the amount of supplementary food available to bears, along with varying weather conditions, are the main factors affecting the probability of winter bear observations. Understanding this relationship is essential to predict future effects of climate change and supplementary feeding on brown bears denning ecology. In the current study, our objectives were: (1) to document the spatial and temporal patterns in the occurrence of brown bear winter observations over a 30-year period, (2) to disentangle the relationship between the probability of brown bear observations, weather conditions, and supplementary feeding in winter.

2. Materials and methods

2.1. Study area

We conducted the study in the northeastern part of the Carpathians, the Bieszczady Mountains (SE Poland, N 49.23° E 22.58°, Fig. 1). The area encompassed about 2500 km^2, with altitudes ranging between 400 and 1340 m a. s. l. Forest covered ca. 70% of the area and consisted mainly of beech *Fagus sylvatica* and silver fir *Abies alba*, with admixtures of Norway spruce *Picea abies*. The major part of the study area, except for Bieszczady National Park (290 km^2), was managed by the Polish State Forestry for the purposes of timber harvesting and hunting. The managed part of the study area was divided into forestry management units, the State Forest Districts (112–548 km^2, Fig. 1). Game management involved intensive year-round supplementary feeding of ungulates with hay, corn, sugar beets and oats at established locations distributed uniformly across the forested areas outside the national park (average density 14 sites per 100 km^2, Selva et al., 2017, 17.5 sites per 100 km^2 excluding the national park area). The annual amount of supplementary food provided for ungulates by the State Forest Administration during the hunting seasons 1993/1994–2015/2016 ranged from 150 to 815 tons (data from the Regional Directorate of the State Forest Administration in Krosno).

The human population density was ca. 16 persons per 1 km^2 (Central Statistical Office, 2012). The mean annual temperature during the 30 years of study was 7.3 °C and average annual precipitation was 909 mm (Institute of Meteorology and Water Management, Poland). Mean daily temperature in January–February across six meteorological stations and over 30 years was −2.4 °C and ranged from 1.3 °C to −8.8 °C. Average depth of snow cover in January and February during the study period was 14.3 cm (1.4–39.6 cm, varying with the location and year). There were 15–60 (average 44) days with snow cover in those two months.

The large-mammal community consisted mainly of four ungulate species: red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, wild boar *Sus scrofa* and European bison *Bison bonasus*; and three species of large carnivores: brown bear, wolf *Canis*

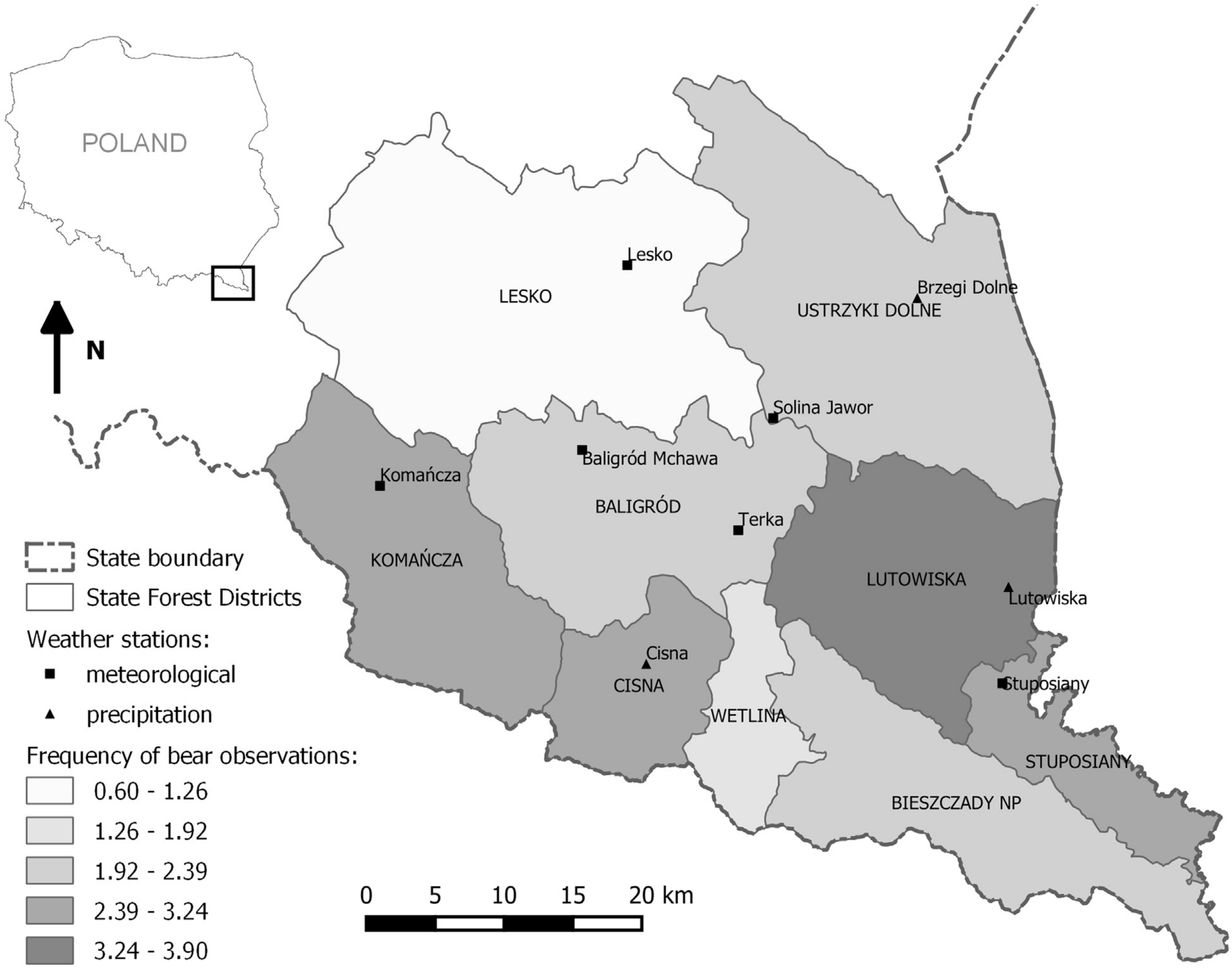

Fig. 1. Study area with the locations of weather stations (meteorological and precipitation) in the Bieszczady Mountains (SE Poland, Northeastern Carpathians) where data on brown bear winter observations were collected in 1987–2016. Frequency of bear observations is expressed as the mean annual number of 10-day periods in January and February when signs of bear activity were recorded (maximum possible number of 10-day periods = 6) in each State Forest District and Bieszczady National Park.

lupus and Eurasian lynx *Lynx lynx*. Bear numbers in the study area were estimated at 35–50 in 1990–1991 (Frąckowiak and Gula, 1996; Gula and Frąckowiak, 2000) and at 46–83 individuals in 2009–2010 (Selva et al., 2011; Śmietana et al., 2014). Brown bears are strictly protected in Poland.

2.2. Data on brown bear winter observations and numbers

The data on brown bear winter observations and numbers were obtained via a questionnaire-based monitoring of the brown bear in Poland in 1987–2016. Each year the questionnaires were sent to nine areas: eight State Forest Districts (Baligród, Cisna, Komańcza, Lesko, Lutowiska, Stuposiany, Ustrzyki Dolne, Wetlina) and to Bieszczady National Park. The State Forest Districts of Cisna and Wetlina were merged in 2010 but continued to provide separate sets of data. The State Forest Districts and the National Park were divided into 7–18 smaller forest subunits each, of area 15–34 km^2. Every forest subunit (in total 104) was managed by two foresters hired by the forestry administration, who spent most of their working time (40 h a week) in the forest, patrolling their unit on every working day (except for the weekends), all year round, regardless of the weather. In addition, the hunting officers responsible for game management in the State Forests Districts regularly patrolled the whole area to provide food at supplementary feeding sites and organize hunting activities. The forestry personnel (foresters and hunting officers) collected the data on signs of bear presence (including direct observations, footprints, signs of foraging, scats) throughout the year.

Data concerning bear winter observations were collected by foresters and hunting officers for two months each winter, the entirety of January and February. Assuming that all the foresters involved in the data collection spent 75% of their working hours in the field, the total data collection effort in January and February was ca 50,000 h. In the questionnaire, forestry personnel were required to report whether they observed any signs of bear activity in each of six periods as followed (later called 10-day periods): 1–10th, 11–20th and 21–28/29/31st of January and February. The data were recorded in a binary form, with 1 indicating presence of any sign of bear activity in each 10-day period, and 0 indicating lack thereof. The questionnaires were sent once per year to a national coordinator, who transferred the data from small forest subunits to a spatial scale of the State Forest Districts/ Bieszczady National Park. Therefore, bear activity was considered to occur during a 10-day period in a given area if it was observed at least once in at least one of the small forest subunits belonging to that area. Throughout the 30 years of study we received full sets of questionnaire answers on winter bear observations from nearly all the areas (excluding two questionnaires from one State Forest District in 2011 and 2014), accounting for 269 questionnaires, each consisting of six 10-day periods (N = 1614).

The questionnaire data were also used to assess the number of bears in the study area, in order to provide an index used to relate the frequency of bear winter observations to trends in their overall numbers. This index was calculated based on systematic, year-long observations of bears and signs of their presence conducted by foresters and hunters (Zyśk-Gorczyńska et al., 2016). All available information on bear occurrence within each State Forest District/Bieszczady National Park, i.e. casual observations, measured footprints, snow tracking, dens, observations of females with cubs, were provided to a coordinator (a biologist or a wildlife specialist) of that area along with detailed information on time and location. The game specialists in each area prepared expert assessments on bear numbers once every year. The results were submitted to the national coordinators, who re-examined all data. Four State Forest Districts (Baligród, Cisna, Komańcza, Stuposiany) and Bieszczady National Park delivered the most complete information on bear numbers, therefore we only used these data in the analyses (Fig. 1). The final index of bear numbers that we used as an explanatory variable in the analyses was a sum of number of individuals across those five areas. The questionnaire forms for both bear numbers and their observations in January–February did not change over years.

2.3. Statistical methods

We obtained data on daily weather conditions: mean temperature, precipitation and depth of snow cover from six meteorological stations and three precipitation stations administered by the Institute of Meteorology and Water Management (Fig. 1). To relate bear observations to weather conditions, we used the data from meteorological stations located the closest to the centre of the area where bear activity was reported (Supplementary Material Table S9). In cases where a precipitation station was located closer to an area than a meteorological station, we used the precipitation data (precipitation and snow cover depth) from that station. We calculated the mean, minimum and maximum values of temperature, precipitation and snow cover for each 10-day period of January and February and the last 10-day period of December. We used sunrise and sunset tables (http://www.cmpsolv.com/los/sunset.html) to define the average day length, as the time from sunrise to sunset, for each 10-day period. The data on supplementary feeding were provided by the Regional Directorate of the State Forests in Krosno as the annual (per hunting season: March–February) amounts of feed (hay, maize, sugar beets, oats) per each State Forest District since 1994. As bears do not consume hay, we excluded this type of feed, and calculated the amount of supplementary food provided per km^2 in each State Forest District and year.

Weather data included several strongly inter-correlated variables. Thus, in the first step we attempted to reduce the dimensionality of weather parameters using principal component analysis (PCA). PCA was performed in two sub-groups of variables: we separately transformed variables describing current weather conditions, and separately variables describing conditions from the preceding 10-day period. Weather variables were scaled to unit variance and zero mean, and in cases where significant deviations from normality were observed, we transformed the data appropriately. Transformations (natural logarithm) were necessary in variables describing precipitation (average, maximum, minimum) and snow cover depth (average, maximum, minimum).

Prior to PCA, we determined the optimal number of components to extract using the *nFactors* library in R (R Core Team, 2017). The analysis suggested extracting four components for the current weather conditions and two components from the previous 10-day period's weather conditions. Extracted components (see Results) were merged with original data. One of the components (the first component of the previous 10-day period conditions) was inverted (multiplied by −1) to make it easier for interpretation (that way an increase in this component means an increase in average temperature; see Table 1).

Patterns of bear winter observations (binary scores: 0 = not observed, 1 = observed) were analyzed using generalized linear mixed models with a logit link function and binomial error distribution (package *lme4*). Each model included the following fixed effects: all six principal components, categorical factors of month (January, February) and 10-day period (within each month, the 1st, 2nd and 3rd 10-day period) plus an interaction between the month and the 10-day period, and a continuous year effect. A subset of models was also considered where year was replaced with the yearly number of recorded bears. Due to perfect collinearity of the year and the number of individuals we were unable to include both variables in a single model. Additionally, each model included a random effect of the identity of the area (State Forest District or Bieszczady National Park) from which data were collected.

The size of area (State Forest District/Bieszczady National Park) could positively influence the probability of observing bears because larger areas potentially included more individuals and hired more forestry personnel members, resulting in a higher survey effort. To account for this, we ran an additional analysis where the size of the area was included as an explanatory variable. Analysis of models jointly accounting for size of the area and for its identity as a random effect was not possible - since both factors explain similar information in the data, most of the models including both terms failed to

Table 1
Principal components (PC) of the current (during a given 10-day period) and previous (during the preceding 10-day period) weather variables in the Bieszczady Mountains, SE Poland, in 1987–2016. Principal components were extracted by restricting the calculated PCs to those exhibiting eigenvalues larger than unity. Values represent loadings of original variables (first column) on the principal components. Names in brackets indicate the interpretation of each component.

Current conditions	PC1 (Snow cover)	PC2 (Precipitation)	PC3 (Day length)	PC4 (Temperature)
Average temperature	−0.45	0.11	0.31	0.79
Average temperature amplitude	0.01	−0.20	0.34	−0.84
Average precipitation	0.04	0.97	0.04	0.15
Average snow cover	0.96	0.01	0.03	−0.20
Average day length	0.14	0.08	0.90	−0.04
Maximum temperature	−0.49	0.02	0.55	0.52
Maximum precipitation	−0.03	0.97	0.06	0.06
Maximum snow cover	0.94	0.09	0.02	−0.12
Minimum temperature	−0.39	0.04	0.14	0.85
Minimum precipitation	0.83	−0.11	0.05	−0.33
Previous conditions	**PC1 (Prev. temperature/ snow cover)**	**PC2 (Prev. precipitation)**		
Average temperature	−0.90	0.16		
Average temperature amplitude	0.61	−0.35		
Average precipitation	−0.14	0.92		
Average snow cover	0.84	0.36		
Average day length	0.08	0.26		
Maximum temperature	−0.78	0.06		
Maximum precipitation	−0.12	0.88		
Maximum snow cover	0.75	0.46		
Minimum temperature	−0.85	0.13		
Minimum precipitation	0.83	0.14		

converge. We therefore present the results of the analyses including the area identity (and not its size) in the Results section, whereas the results including the area size are presented in the Supplementary material (Tables S5 − S8).

Because the data on the amount of supplementary food were available since 1994, we ran the analyses based on two datasets: for the years 1987–2016 and for 1994–2016, including the yearly amount of supplementary food per km^2 in each area as an additional explanatory variable only in the latter analysis. Since supplementary feeding was not conducted in Bieszczady National Park, this area was excluded from the second analysis.

Due to a considerable number of model predictors, we used model selection to find the most optimal model in all sets of data. Selection was performed using the *MuMIn* package and was based on the Akaike Information Criterion (AICc). We have considered models differing from the best model (the one with the lowest AIC) by less than 2 AIC units as comparable ones. To extract unbiased estimates of parameters from such a set of optimal models, we have averaged fixed effect estimates over the preselected set of top models.

3. Results

We recorded signs of bear activity in January and February in each of the 30 years of the study. As every year the bear observations were recorded in six 10-day periods in each of nine areas, the maximum frequency of bear observations (100%) in the whole study area occurred when bear activity was recorded 54 times during a year. Accordingly, the frequency of bear observations ranged from 5% in 2005, when bear activity was observed in three areas during only one 10-day period each, to 91% in 2012, when active bears were recorded in all the areas during at least five 10-day periods (Fig. 2). The mean frequency of bear observations in the study period varied throughout the area, from less than one 10-day period per winter in Lesko Forest District to almost four 10-day periods in Lutowiska (Fig. 1). There was a general increasing trend in frequency of observations of bear activity throughout the study area, which correlated positively with the number of bears reported (Fig. 2). The ambient temperature in 10-day periods when signs of bear activity were not observed was generally lower (mean −2.8 °C) and snow cover was deeper (mean 17.4 cm) than during 10-day periods when bears were active (−1.9 °C and 14.0 cm, respectively).

In both sets of models (including year and including the number of bears) all individual models achieved convergence. Apart from year/number of bears, in both sets of models three variables had the highest impact on probability of bear observations: snow cover PC, temperature/temperature amplitude PC and month (Tables 2 and 3). Additionally, in the restricted dataset (from 1994) the amount of supplementary food positively affected the probability of observing bears (Table 3). Observed effect sizes were almost identical in both sets of models: the probability of observing active bears was negatively related to the given 10-day period's depth of snow cover (Table 3, Fig. 3a), and positively related to its ambient temperature (Table 3, Fig. 3b). Bears were more likely to be observed in February (Tables 2 and 3), however statistical significance of this effect was lost when performing full model averaging (instead of conditional model averaging).

Results obtained using models where the random term of area identity was replaced by its size were qualitatively identical to those presented above (see Supplementary Tables S5 − S8). We detected no effect of the area size.

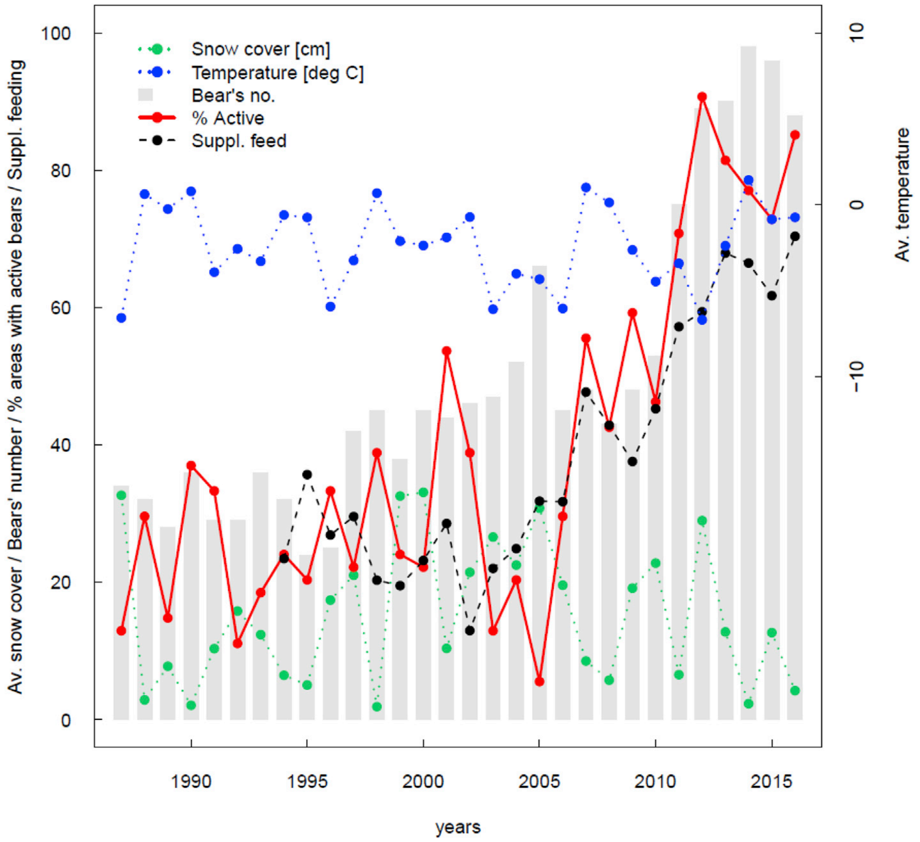

Fig. 2. Mean ambient temperature and snow cover depth, amount of supplementary food ($10 \times$ tons/km^2, data available from 1994), estimated brown bear numbers and frequency of bear observations (% of 54 = 9 areas x 6 10-day periods) in the Bieszczady Mountains, Poland, in January and February 1987–2016.

Table 2
Model-average estimates from the models (see Table S1 for the list of best models) describing the probability of brown bear activity in January and February 1987–2016 in the Bieszczady Mountains, SE Poland. Models include the year instead of number of bears (see Table S3 for relevant estimate including number of bears). We provide coefficient estimates (for 10-day period two estimates are contrasts with the intercept) and their standard errors, Z values, associated type-I error p-values calculated from model-selection tables. Model terms are principal components calculated based on weather variables (Table 1).

Model term	Estimate	SE	Adjusted SE	Z value	P
(Intercept)	−0.789	0.300	0.300	2.632	0.008**
Day length	0.107	0.115	0.115	0.934	0.350
Prev. precipitation	−0.087	0.081	0.081	1.063	0.288
Prev. temperature/snow cover	−0.173	0.095	0.095	1.814	0.070.
Year	1.001	0.071	0.071	14.153	<0.001***
Snow cover	−0.274	0.097	0.097	2.817	0.005**
Temperature	0.104	0.070	0.070	1.487	0.137
Precipitation	−0.044	0.063	0.063	0.691	0.489
Month (February)	0.205	0.218	0.218	0.938	0.348
10-day period (2nd)	0.023	0.083	0.083	0.280	0.780
10-day period (3rd)	0.026	0.090	0.090	0.289	0.773

4. Discussion

Using 30 years of data, we demonstrated that factors associated with global change, namely winter weather conditions and supplementary feeding, affect the probability of observing brown bear activity in winter. Ambient temperature and the depth of snow cover were the most important weather determinants of the spatio-temporal variation in probability of bear observations. Weather conditions affect denning behavior in brown bears at the physiological level (Tøien et al., 2011; Evans et al., 2016), and they seem to be particularly important in determining the timing of den exit (Pigeon et al., 2016). Additionally, low ambient temperature and deep snow cover increase the energy expenditure during locomotion, restricting bears' activity (Parker and Robbins, 1984; Hobbs, 1989; Parker et al., 1999). The amount of supplementary food was another

Table 3
Model-average estimates from the models (see Table S2 for the list of best models) describing the probability of brown bear activity in January and February 1994–2016 in the Bieszczady Mountains, SE Poland. Models include the year instead of number of bears (see Table S4 for relevant estimate including number of bears). We provide coefficient estimates (for 10-day period two estimates are contrasts with the intercept) and their standard errors, Z values, associated type-I error p-values calculated from model-selection tables. Model terms are principal components calculated based on weather variables (Table 1) and amount of supplementary food.

Model term	Estimate	SE	Adjusted SE	Z value	P
(Intercept)	−0.406	0.337	0.338	1.204	0.229
Day length	0.013	0.130	0.130	0.100	0.920
Prev. precipitation	−0.023	0.060	0.060	0.378	0.705
Prev. temperature/snow cover	−0.015	0.059	0.059	0.254	0.799
Year	0.976	0.099	0.099	9.818	<0.001***
Snow cover	−0.360	0.095	0.095	3.799	<0.001***
Temperature	0.169	0.080	0.081	2.092	0.036*
Precipitation	−0.054	0.081	0.081	0.669	0.504
Supplementary feeding	0.349	0.139	0.139	2.512	0.012*
Month (February)	0.415	0.280	0.281	1.479	0.139
10-day period (2nd)	0.189	0.242	0.242	0.782	0.434
10-day period (3rd)	0.182	0.250	0.250	0.728	0.467

important factor affecting the probability of bears' winter observations in our study area. Thus, the abundance of human-derived forage and mild to moderate weather seem to explain why bears do not den. Bears in our study area also use natural resources (such as ungulate remains from wolf kills) in winter (Bojarska, 2014). However, finding these resources usually requires extensive mobility and may constitute an overly high energetic challenge in deep snow and low temperatures. Supplementary food, on the other hand, is predictable in space and time, and feeding sites can be easily accessed via a network of forest roads, some of which are cleared of snow. Thus, feeding on supplementary food can be beneficial in terms of energy gain for bears in moderate or even harsh weather conditions, when foraging on other food sources becomes unprofitable. This effect might be reciprocal: bears that stay active during energetically demanding weather plausibly rely more on supplementary food. Therefore, this situation might act as an ecological trap, for example if the weather conditions suddenly deteriorate and bears are not able to resume denning fast enough to avoid high energy loss. Bears in areas with very mild winters often stay active or den only for short periods (Huber and Roth, 1997). Whether supplementary fed bears would also be active in response to more severe weather conditions if supplementary food was not available, remains an open question. Our results agree with several other studies that suggested a strong link between brown bear behavior in winter and supplementary feeding (Frąckowiak and Gula, 1996; Kavčič et al., 2015; Krofel et al., 2017; Selva et al., 2017).

Regular observations of bear activity in January and February suggest that some individuals in our study area either interrupted their denning, denned only shortly or did not den at all. This phenomenon was progressively evident over the 30-year period of our study, suggesting that milder winters, intensification of supplementary feeding, and growing bear numbers will likely contribute to an increase of frequency of observations of winter-active individuals in the future. Strong positive relationship between the probability of bear observations and year most likely results from a year to year increase in the number of individuals, a phenomenon observed in the study area since 1950 (Gula and Frąckowiak, 2000; Zyśk-Gorczyńska et al., 2016). Bear numbers included in our analysis were undoubtedly biased due to methodological errors related to observation-based assessments, e.g. counting the same individuals by personnel of different State Forest Districts (Gula and Frąckowiak, 2000) but should nonetheless represent a reliable index of a year-to-year trend in bear counts (Zyśk-Gorczyńska et al., 2016). Observational data on brown bears have been proved to serve as an accurate method in brown bear monitoring when sufficient effort is applied and data are collected by trained observers (Kindberg et al., 2009). The method was used to assess the trends in bear numbers and proved useful to the long-term monitoring of the brown bear, providing official statistics on the population metrics of this species in Poland (Boitani et al., 2015). The increase of bear population is corroborated by less systematic but more methodologically reliable counting in our study area (Selva et al., 2011; Śmietana et al., 2014), and has been observed also in neighboring countries (Khoyetskyy, 2013; Chapron et al., 2014).

The increase in frequency of brown bear observations may be additionally associated to other factors. Intensification of logging and associated development of forest roads observed in recent years in the study area implicates more human disturbance and facilitated access to areas at higher elevations, usually used by bears for denning, which may cause more frequent den abandonments (Frąckowiak and Gula, 1996; Linnell et al., 2000; Elfström et al., 2008). Moreover, the development of forest roads may be accompanied by establishment of new supplementary feeding sites, thus expanding their network into hitherto not supplemented areas. Finally, as the foresters mainly use the forest roads to move across the area, the expansion of road network results in an intensification of search effort, further contributing to the increase in frequency of bear observation. Otherwise, the survey effort (measured in man-hours) remained relatively constant over the study period, as the division of the study area into forest subunits and the number of forestry personnel remained relatively constant. There was a variation in search effort between areas related to their size, but the effect of the area size on probability of observing active bears did not appear significant.

Our results on bear activity may be biased due to false negatives, i.e. active bears might have been not always detected by forestry personnel. Nevertheless, in our opinion the importance of this bias was negligible thanks to the intensive use of

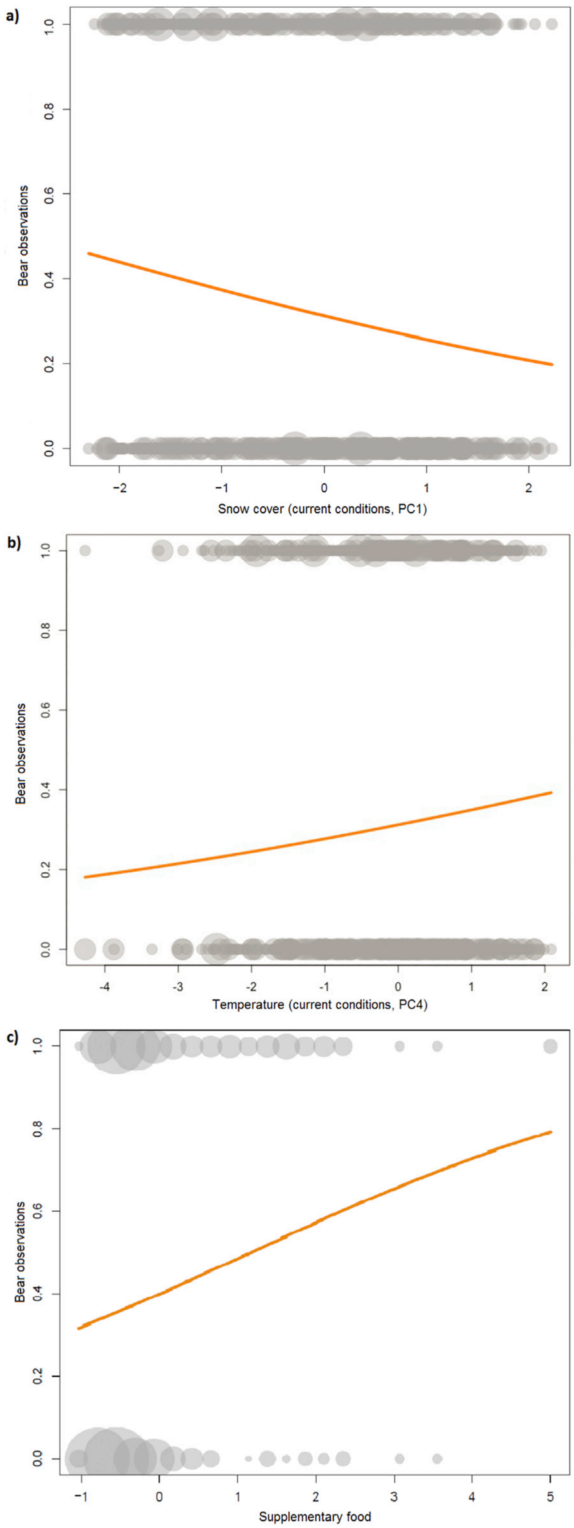

Fig. 3. Probability of observing signs of brown bear activity in January and February in the Bieszczady Mountains, Poland (1987–2016) in relation to a) mean snow cover depth, b) mean ambient temperature and c) the amount of supplementary food (the supplementary feeding data available since 1994).

feeding sites and forest roads by both bears (Selva et al., 2017) and foresters, and due to snow cover enabling easy recognition of bear tracks. What is more, the binary form of the response variable (presence of bear signs) guaranteed that even one observation in a given 10-day period, recorded in only one of 7–18 small forest subunits, was enough to classify bears as active in the whole State Forest District/Bieszczady National Park, which makes false negatives less likely. The lack of snow cover might cause an opposite bias in the results, as bear tracks could be more difficult to detect. Despite that, the snow cover depth still had a negative influence on probability of bear observation, probably because snow was present during three quarters of the winter on average, which mitigates this potential impact on our results.

Our study presents further evidence on the impact of climate change and artificial food provisioning on wildlife. The results provide new insight into the mechanism on how weather variables and anthropogenic food subsidies affect the brown bear, a species considered as threatened by climate change and human activity (Albrecht et al., 2017). While winter activity of bears observed in this study seems to be an appropriate behavioural response to mild weather, the role of supplementary food in shaping this behavior rises a deeper concern. The abundance of this artificial resource, coupled with its non-natural spatial and temporal patterns of availability, may considerably alter bear behavior. Our results indicate that availability of supplementary food interacts with the natural relationship between weather conditions and cost-effectiveness of foraging in bears. Climate change projections predict milder winters (Jacob et al., 2014) and thus we can expect more bears to be active in winter throughout the species' range. This pattern will probably be more pronounced in areas where supplementary feeding is practiced. In these areas, the dependence of bears on supplementary food might increase in the future. Limiting the amount of food provided to wildlife may be an important way to mitigate the anthropogenic influence on brown bear behavior.

Acknowledgments

The questionnaire survey regarding bear activity and numbers was conducted within the brown bear monitoring program by the Institute of Nature Conservation of Polish Academy of Sciences. We thank the foresters and administration of State Forest Districts of Baligród, Cisna, Lesko, Lutowiska, Komańcza, Stuposiany, Ustrzyki Dolne and Wetlina, and Bieszczady National Park, who collected the information on bear activity in the field and completed the questionnaires. Regional Directorate of the State Forests in Krosno provided data on supplementary feeding. This work was supported by the Institute of Nature Conservation of Polish Academy of Sciences through the Institute's statutory funds. We thank Luca Maugeri for his helpful comments on the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00523.

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